Received: 24 April 2020 | Revised: 18 October 2020 | Accepted: 15 November 2020

DOI: 10.1002/jez.2432

RESEARCH PAPER

JEZ-A ECOLOGICAL AND INTEGRATIVE PHYSIOLOGY WILEY

Ecophysiological models for global invaders: Is Europe a big playground for the African clawed frog?

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Funding information

Eranet Biodiversa / DFG,
Grant/Award Number: RO 4520/3-1

Abstract

One principle threat prompting the worldwide decline of amphibians is the introduction of nonindigenous amphibians. The African Clawed Frog, *Xenopus laevis*, is now one of the widest distributed amphibians occurring on four continents with ongoing range expansion including large parts of Europe. Species distribution models (SDMs) are essential tools to predict the invasive risk of these species. Previous efforts have focused on correlative approaches but these can be vulnerable to extrapolation errors when projecting species' distributions in nonnative ranges. Recent developments emphasise more robust process-based models, which use physiological data like critical thermal limits and performance, or hybrid models using both approaches. Previous correlative SDMs predict different patterns in the potential future distribution of *X. laevis* in Europe, but it is likely that these models do not assess its full invasive potential. Based on physiological performance trials, we calculate size and temperature-dependent response surfaces, which are scaled to geographic performance layers matching the critical thermal limits. We then use these ecophysiological performance layers in a standard correlative SDM framework to predict the potential distribution in southern Africa and Europe. Physiological performance traits (standard metabolic rate and endurance time of adult frogs) are the main drivers for the predicted distribution, while the locomotor performance (maximum velocity and distance moved in 200 ms) of adults and tadpoles have low contributions.

KEYWORDS

amphibian, distributional modelling, ecological niche theory, fundamental niche, invasive species management, mechanistic model, nonnative range, physiological adaptation, species distribution models

1 | INTRODUCTION

Amphibians are the most threatened vertebrate class suffering worldwide dramatic population declines in the last decades (Gonzalez-del-Pliego et al., 2019; Wake & Vredenburg, 2008). Nearly 50% of amphibians are estimated to be threatened by extinction (Gonzalez-del-Pliego et al., 2019). One main threat is the introduction of other invasive amphibians (Blaustein et al., 2011; Measey et al., 2016; Nunes et al., 2019) like the African Clawed Frog, *Xenopus laevis* (Daudin, 1802), which has both a direct negative impact on the indigenous invertebrate and amphibian fauna (Courant et al., 2017; Courant et al., 2018; 2018; Lillo et al., 2011; Vogt et al., 2017), and indirect impact as a potential reservoir for chytridiomycosis (Solis et al., 2010).

The African Clawed Frog, *X. laevis*, is a principally aquatic species native to southern Africa (Measey et al., 2012). In the past, *X. laevis* has

been extensively used for human pregnancy testing and was distributed pan-globally for laboratory research (Gurdon & Hopwood, 2003; van Sittert & Measey, 2016), and pet trade (Herrel & van der Meijden, 2014; Measey, 2017). Escapees and voluntarily released individuals have resulted in numerous invasive populations outside its native range, and today *X. laevis* is recognized as one of the world's most widely distributed amphibians occurring on four continents (Ihlow et al., 2016; Measey et al., 2012; Wang et al., 2019). For instance, in Europe it was successfully introduced to France (Fouquet, 2001), Portugal (Rebelo et al., 2010), and Italy/Sicily (Lillo et al., 2005) and further expansions up to more than 1 Million km^2 in Europe are predicted (Measey et al., 2012).

The identification of conditions limiting a species' distribution is particularly important for the assessment of invasion risk (e.g., Jimenez-Valverde et al., 2011; Kearney et al., 2008). For this task, species distribution models (SDMs) can be a useful tool. Important for SDMs is the concept of the ecological niche. The ecological niche is a combination of abiotic (fundamental) and biotic factors (interactions among taxa such as competition, parasitism, mutualism, predator-prey-relationship, etc.). The fundamental niche contains all abiotic factors that are necessary for species persistence and reproduction (Grinnell, 1917; Hutchinson, 1978; Soberón & Peterson, 2005; Soberón, 2007). Climate is one of the main factors driving the ecological niche and potential distribution of a species (Soberón, 2007; Thuiller et al., 2004). This also seems to be the case for invasive anurans that establish and spread in areas matching their native climatic conditions (Rago et al., 2012; Tingley et al., 2010).

Previous efforts to predict the potential distributions of invasive amphibians across space and time (Ficetola et al., 2007, 2010; Kolbe et al., 2010; Nori et al., 2011) have mainly focused on correlative SDMs that statistically link geographic occurrences to environmental conditions (Dudik et al., 2004; Kearney & Porter, 2009; Peterson et al., 2015). It has been shown that projections of correlative SDMs from the native to a nonnative area are sometimes unable to predict the entire range which could be occupied by a species. This make predictions of future distributions for species questionable (Broennimann et al., 2007).

More recently, process-based approaches like mechanistic or ecophysiological SDMs that determine mechanistic interactions between aspects of the fitness of organisms and their environment have been developed to predict species distributions (Ceia-Hasse et al., 2014; Kearney & Porter, 2009). They have since been applied to lizards (e.g., Buckley, 2008; Kearney & Porter, 2004; Sinervo et al., 2010), freshwater invertebrates (e.g., Gilman et al., 2006), plants (e.g., Case & Lawler, 2017) and invasive amphibians (e.g., Kearney et al., 2008; Kolbe et al., 2010). In contrast to correlative SDMs, mechanistic SDMs are trained by data assessed under laboratory conditions (e.g., critical thermal limits), and do not correlate spatially implicit physiological layers with knowledge of occurrence records (Kearney et al., 2008). Hybrid models combine process-based and correlative approaches by using the output of the first as input for the latter (Buckley et al., 2011). Hybrid and process-based models are more data intensive and require more knowledge of the ecology and physiology of a species (Thuiller, 2007). They are constrained by availability of data and the identification of adequate key processes limiting species distributions (Elith et al., 2010). Process-based and hybrid SDMs emphasize those processes involved in determining range constraints (Morin & Thuiller, 2009), and as such they are more robust in terms of space and time (Elith et al., 2010) because they try to assess the fundamental (climatic) niche.

In ectothermic organisms such as amphibians, physiological performance is strongly influenced by environmental parameters, impacting physiological processes such as muscle contraction (James et al., 2012) and ultimately affecting performance traits such as locomotion (Feder & Burggren, 1992; Herrel & Bonneaud, 2012a; Wilson et al., 2000). The close dependence of ectotherms on environmental conditions (Miller et al., 2004; Parmesan & Yohe, 2003; Sinervo et al., 2010) makes amphibians ideal subjects for species distribution modelling.

Previous maximum entropy (Maxent) models based on native and invasive species records were used to predict suitable areas for *X. laevis* on a global scale (Ihlow et al., 2016; Measey et al., 2012). The Maxent and ensemble SDMs of Ihlow et al. (2016), however, projected a broader suitable distribution than the Maxent models of Measey et al. (2012). A recent hypervolume model, trained with the complete set of species records across the globe and based on PCA relying on 19 bioclimatic variables, predicted a fragmented distribution of *X. laevis* across the invaded range (Rödder et al., 2017). Additionally, the hypervolume models' projected distribution in southern Africa resembles the species' current natural distribution well.

Although all of these correlative SDMs predict quite different patterns in the potential distribution across Europe, it is likely that these models do not predict the full invasive potential of this species. Increased funding (for instance by INVAXEN [Invasive biology of *X. laevis* in Europe: ecology, impact, and predictive models]) and resultant laboratory research have resulted in a copious amount of literature and provided input data for models (van Wilgen et al., 2018). For example, field and laboratory research has provided information on environmental constraints affecting the species' diurnal and annual activity patterns, reproduction, and thermal tolerances (De Villiers & Measey, 2017; Eggert & Fouquet, 2006; McCoid & Fritts, 1989; Measey, 2016; Wilson et al., 2000). These studies indicate that *X. laevis* is a species with a strongly underestimated invasive potential.

Temperature affects physiological traits, such as digestive and locomotive performance, and is one of the most important extrinsic factors affecting the biology of ectotherms (Angilletta et al., 2002; Bennet, 1990; Huey & Kingsolver, 1989). In pipid frogs, such as *X. laevis*, temperature affects fitness-relevant traits like reproduction, larval development (Balinsky, 1969), endurance capacity (Herrel & Bonneaud, 2012a), sprint performance (Miller, 1982), and swimming velocity (Herrel & Bonneaud, 2012a; Wilson et al., 2000), of adults and tadpoles (Wilson et al., 2000). Additionally, these physiological traits give an indicator for energy use and balance, and are critical traits in amphibian biology (Wygoda, 1984). Here we use ecophysiological models to assess the potential distribution of the African Clawed Frog, *X. laevis*, across Europe, and compare relevant performance traits of tadpoles and adult frogs from the native population.

TABLE 1 Performance variables and their abbreviations

Full variable name	Abbreviation	Description
Maximum velocity	MaxVel	Maximum swimming velocity
Distance moved in 200 ms	D200	Distance moved in 200 ms
Endurance distance	EndurDist	Distance moved until animal is exhausted
Endurance time	EndurTime	Time until animal is exhausted
Standard metabolic rate	SMR	Standard metabolic rate of an animal
Evaporative water loss	EWL	Water loss of an animal due to evaporation
Hours of activity	h_a	Daily hours when performance is possible
Hours of restriction	h_r	Daily hours when performance is not possible
Critical thermal minimum	CT_{min}	Minimum temperature at which performance of an animal is 0
Critical thermal maximum	CT_{max}	Maximal temperature at which performance of an animal is 0
Optimum temperature	T_{opt}	Temperature at which performance is at its maximum
Predicted performance	Pred_perf	Predicted performance at T_{opt}

2 | METHODS

2.1 | General methodological approach

Based on the results of physiological performance trials (for performance variables and their abbreviations see Table 1), we computed temperature (for tadpoles and adults) and body-size dependent (adults only) response surfaces characterizing the performance of tadpole and adult *X. laevis* in geographic space. These surfaces were scaled to a range matching the physiological limits (critical thermal minimum and maximum, CT_{min}, CT_{max}). Environmental layers were then used to assess the predicted performance of the species in geographic space. These ecophysiological performance layers were subsequently used in a popular correlative SDM framework to predict the potential distribution of *X. laevis* in southern Africa and Europe.

2.2 | Selection of specimens and traits

Phylogeographic studies assume the most likely origin for most invasive populations in Europe is the south-western Cape of South Africa's winter rainfall region (De Busschere et al., 2016), which is supported by climate matching analyses (Rödder et al., 2017) and export records (Measey et al., 2020; van Sittert & Measey, 2016). However, the French invasive population consists of a mixture of clades from both of South Africa's winter and summer rainfall regions (De Busschere et al., 2016). Thermal performance trials were made on adult frogs collected in Port Elizabeth Eastern Cape province, which could be characterized as an all year round rainfall region, indicative of the southern Cape region. It is located between both regions, and has genetic clades representing both areas (Measey et al., 2017). For thermal performance trials of tadpoles, we used tadpoles bred from adult frogs sampled from Stellenbosch and Potchefstroom, South Africa. Stellenbosch, Western Cape province, is an area in the winter rainfall region, while Potchefstroom, north-west province, was chosen to represent the summer rainfall region.

Under laboratory conditions, the following physiological performance data were determined for adult frogs: burst swimming performance measured as maximum velocity (MaxVel), evaporative water loss (EWL), standard metabolic rate (SMR), endurance time (EndurTime) and endurance distance (EndurDist). For tadpoles, the following physiological performance data was assessed: maximum velocity (MaxVel) and distance moved in the first 200 ms (d200) after a startle response.

2.3 | Locomotor performance of adult frogs

The performance trait maximum velocity (MaxVel) was chosen because it provides an indicator for burst performance, important in contexts of prey capture and predation avoidance. Adult *X. laevis* were kept at 20°C. Swimming speed performance traits were recorded by randomly choosing 10 individuals (5 males and 5 females) for each temperature trial from a pool of 30 individuals. Performance trials were conducted in a climate chamber, ranging from ambient temperatures of 10°C, 15°C, 20°C, 25°C, and 30°C (Herrel & Bonneaud, 2012a, 2012b; Wilson et al., 2000). Before conducting the trials, the climate chamber was set overnight to reach the target temperature and the trials were started only when the temperature was within a 1°C range, measured with a thermocouple thermometer in the climate chamber (Fluke 54IIB, Fluke Corporation, Washington). To minimize any effect of a directional shift in temperature on performance, the sequence of target temperatures was randomly determined. One hour before the trials started frogs were placed in separate boxes with water in an incubator set at the test temperature (Navas, 1996). All performance trials were iterated twice for each individual animal with an intertrial period of one hour, during which

specimens were removed to the incubator to be retained at the target temperature allowing recovery. Experiments were conducted in a transparent Perspex tank (2.0 m × 0.4 m × 0.4 m), which was marked at 25 cm steps. A mirror with size 1.4 m × 0.4 m was assembled at a 45° angle above the tank to make sure that during experiments, frogs were visible from dorsal and lateral aspects. Only the best aspect was used for processing.

A high-speed digital video camera (Canon *PowerShot* G15, Canon Inc.) set at 240 frames s^{-1} (fps) was used to assess burst swimming performance. A light tap on the urostyle was used to initiate swimming. The video clips were cut to contain at least two movement cycles and then analyzed manually. The image tracking software Blender (version 2.74; Blender Foundation) was used to digitize the snout tip and track it across all frames that successfully captured the two movement cycles. The coordinates of the frog were imported in Excel (Microsoft) and the displacement of the individual along its trajectory was computed. An adapted version of Winter (2005) zero phase shift low-pass Butterworth filter version 2 with the cut-off frequency set at 30 Hz was used to smooth the raw displacement profile. Peak instantaneous velocity was computed by numerical differentiation of the smoothed displacement profiles. The maximum velocity across all swimming sequences assessed were extracted for each specimen at each temperature. Thus, maximum velocity may come from different swimming performance trials (Herrel & Bonneaud, 2012a, 2012b; Herrel et al., 2012, 2014).

2.4 | Physiological performance of adult frogs

The physiological variables evaporative water loss (EWL), standard metabolic rate (SMR), endurance time (EndurTime), and endurance distance (EndurDist) were used. These variables give an indication of how a species uses energy and balance water loss, which is a critical aspect in amphibian biology (e.g., Wygoda, 1984). An open-flow respirometry system after Lighton (2008) and Steyermark et al. (2005) was used to measure EWL and SMR using a push-through mechanism on non-gravid, post-absorptive frogs during rest (Sinclair et al., 2013). Trials were undertaken at seven temperatures spanning from 5°C to 35°C at 5°C steps (Dunlap, 1971). Eight frogs (four males: four females) were randomly chosen from a pool of 30 individuals for experiments at each temperature and a single trial was conducted on each specimen per temperature step. Individuals were placed separately in appropriately sized air-tight glass metabolic chambers. Metabolic experiments were conducted using Mass Flow respirometry operated on a push-through mechanism. Atmospheric air was scrubbed of water vapor before being passed through the metabolic chambers. Air from the metabolic chambers was sequentially sub-sampled, to record gas concentrations at 20 min intervals, recording an air sample every second. To estimate EWL, we measured water vapor pressure until stability was reached. To ensure that the recorded gas and water vapor readings excluded any sudden movement by the frogs, we used a live video feed to monitor the behavior of the frogs during the experiment. Subsequently, all experimental trials within which animals made sudden movements were excluded from the analysis. An experiment was ended when the temperature trace and water vapor pressure was stable for 20 min or when a frog seemed too distressed to continue with assessment. Experiments lasted no more than 2 h (cf., Mokhatla et al., 2019 for detailed methods and data analysis).

For maximum exertion (endurance) experiments, six adult specimens (three males and three females) were randomly chosen from a pool of 30 for each sprint at five temperatures spanning 10–30°C at 5°C intervals (10, 15, 20, 25 and 30). We chased an individual animal along a 4.7 m circular track until exhaustion. This was expressed as the point at which the individual was not able to right itself when flipped on its back (Herrel & Bonneaud, 2012a, 2012b). Experiments were undertaken on dry surface only. We recorded mass to the nearest 0.01 g before and after the experimental run. Similar to the burst speed performance trials, we made sure that body temperature was within 1°C of the target temperature before trial by recording the cloacal temperature using a thermocouple probe (Fluke 54IIB, Fluke Corporation). The floor of the track was covered with a high friction matting (GECKO® Non-slip matting, Cape Town) to improve traction. For each individual, we recorded both the total distance (EndurDist) and the time (EndurTime) spent moving until exhaustion (Herrel & Bonneaud, 2012b).

2.5 | Locomotor performance of tadpoles

We followed an adapted version of the protocol to measure activity of tadpoles in response to acute temperature designed by Wilson et al. (2000). *X. laevis* tadpoles were lab-reared at 22°C until NF stage 45–47 (Nieuwkoop & Faber, 1994). Developing eggs and tadpoles were kept in 12:12 day:night cycle, fed Frog Brittle® for tadpoles (NASCO), and kept at a high density of 15 specimens L^{-1} to decelerate development (Tejedo & Reques, 1994). For performance trials, ten specimens from each site were chosen for burst swimming speed performance at five temperature levels: 5°C, 10°C, 20°C, 30°C, and 35°C.

Tadpoles were acclimated for the trials by changing the tank water temperature at a rate of 0.2°C min^{-1} until the target temperature was reached. Trials were randomized by assigning random numbers to each trial. We filmed at least five burst swimming responses for each specimen at each specific temperature level to assess burst swimming performance. Each tadpole was only tested once at one test temperature and then euthanized by an overdose of tricaine methanesulfonate (ms-222). The initial burst swimming sequence was filmed with a camera (Olympus, TG-4) at 120 frames s^{-1}. Tadpoles were touched with a fine wire at the tip of their tail to initiate movement. We used a 0.42 m × 0.08 m × 0.17 m clear plastic tank filled with 1 L aged tap water for performance trials. For better visualization of movement by tadpoles in the lateral plane we used a mirror attached to the side of the tank at an angle of 45°. The bottom of the tank was covered with a false bottom where water could circulate through custom-built copper pipes. A water bath (Julabo F12, 4.5 L, max flow 15 L min^{-1}, pressure = 0.35 bar) maintained the desired water temperature.

High-speed videos were filmed from the bottom of the tank and the image in the mirror. All burst swimming sequences were visually proofed and only recordings perpendicular to the filming camera were chosen. We used the motion analysis software Tracker (Open

Source Physics; Brown, 2009) to obtain X and Y coordinates from the high-speed videos. Coordinates were exported to Excel (Microsoft) and the displacement (cm) of the specimen was computed. We chose a fourth order zero-phase shift low-pass Butterworth filter (Winter, 2005) with 12 Hz filter frequency to filter the displacement data. Cut-off frequency was chosen as a 10th of the recording frame rate. From the filtered data, maximum velocity and distance moved in 200 ms were extracted. Temperatures were recorded with a thermocouple (to the nearest 0.01°C).

2.6 | Ecophysiological response surfaces and ecophysiological rasters

Based on information obtained under laboratory conditions we computed temperature and size dependent response surfaces for adults and tadpoles applying the *PerfGAMM2()*-function of the *Mapinguari* package (Sinervo, unpubl.) for R ver. 3.6.2 (R Core Team, 2020). Applying generalized additive models (GAM) with temperature as a smooth predictor and size as linear predictor, the response surfaces were scaled to population-specific critical thermal minimum and maximum by adding these critical thresholds with a performance of zero. By doing so, the data frame used for GAM fitting contained both the performance per temperature step as measured during the experiments and the CT_{min} and CT_{max} values where performance is assumed to be zero. Based on literature CT_{min} was set at 3°C for the native and invasive population and CT_{max} was set at 35°C for the native population and 39°C for invasive population (Courant & Herrel, pers. comm.). Finally, the *PerfGAMM2()*-function estimated the predicted performance (pred_perf) at optimum temperature (T_{opt}) and the critical thermal thresholds (CT_{min} and CT_{max}). As these performance surfaces showed for all variables only very marginal effects of body size for the adult frogs, we subsequently used results for a specimen of 70 mm snout-vent length and translated the respective function in geographic space. For environmental layers we obtained monthly temperature minimum, maximum and averages with a spatial resolution of 2.5 arc min from www.worldclim.org (Hijmans et al., 2005). Furthermore, we computed ecophysiological layers describing the annual hours of activity and hours of restriction by applying the Senoid option in the *EcophysRaster()*-function of the *Mapinguari* package for R (Sinervo, unpubl.). This function simulates daily variation in temperature for each grid cell by computing a sine wave between maximum and minimum temperature at each grid cell and can be used to estimate the annual energetic budget of the species.

2.7 | Species distribution modelling

For data preparation and correlation analyses we used QGIS ver. 3.10 (QGIS Team, 2020), ArcMap ver. 10.6 (ESRI, 2008), R ver. 3.6.2 (R Core Team, 2020) and R's *raster* package ver. 3.0.12 (Hijmans, 2016). As correlative species distribution modelling (SDM) is sensitive to multi-co-linearity of predictors, which can be assumed when measuring the temperature dependence of performance via multiple physiological responses, we computed pairwise Spearman rank correlations between all possible pairs of predictors for tadpoles and adults (Tables 2 and 3). Among pairs with rho exceeding 0.75 we selected only one ecophysiological variable for further processing.

For SDM development we used Maxent 3.4.1 (Elith et al., 2011; Phillips et al., 2006). A total of 616 native species records were compiled from a combination of own field work, and records with > 1 s accuracy from Measey (2004). Modelling range shifts in species such as invasive taxa is especially challenging as in invasive ranges the basic assumption of a range equilibrium with environmental conditions is frequently not met (Elith et al., 2010), which is also the case for invasive populations of *X. laevis* in Europe (Rödder et al., 2017). Therefore, we restricted our analyses to the native range and projected the results onto the European invasive range.

For the environmental background we selected an area defined by a circular buffer of 200 km around each grid cell containing water in southern Africa. For this, global layers containing surface waterbodies that persist at least 50% of the year were obtained from Pekel et al. (2016) in a 30 m resolution and subsequently clipped to get the

TABLE 2 Pairwise Spearman rank correlations among ecophysiological rasters developed based on performance of native adult frogs

	EndurDist	EndurTime	EWL	MaxVel	h_a	h_r	SMR
EndurDist	**1**						
EndurTime	**0.974**	**1**					
EWL	**0.754**	0.721	**1**				
MaxVel	0.095	0.103	0.008	**1**			
h_a	0.116	0.158	0.254	0.057	**1**		
h_r	0.113	0.12	0.002	0.116	0	**1**	
SMR	0.75	0.721	**1**	0.009	0.265	0.002	**1**

Abbreviations: EndurDist, endurance distance; EndurTime, endurance time; EWL, evaporative water loss; h_a, hours of activity; h_r, hours of restriction; MaxVel, maximum velocity; SMR, standard metabolic rate.

Values in bold exceed rho of 0.75.

TABLE 3 Pairwise Spearman rank correlations among ecophysiological rasters developed based on the performance of native tadpoles from the SR (summer rainfall) and WR (winter rainfall) region

	SR d200	SR MaxVel	SR h_a	SR h_r	WR d200	WR MaxVel	WR h_a	WR h_r
SR d200	NA							
SR MaxVel	NA	**1**						
SR h_a	NA	0.221	**1**					
SR h_r	NA	0.003	0	**1**				
WR d200	NA	NA	NA	NA	NA	NA		
WR MaxVel	NA	**0.781**	0.188	0.004	NA	**1**		
WR h_a	NA	0.221	**1**	0	NA	0.188	**1**	
WR h_r	NA	0.003	0	**1**	NA	0.004	0	**1**

Abbreviations: d200, distance moved in 200 ms; MaxVel, maximum velocity; h_a, hours of activity; h_r, hours of restriction; SR, summer rainfall; WR, winter rainfall.

Values in bold exceed rho of 0.75.

waterbody-availability for southern Africa and Europe. We clipped the layers with a high-resolution coastline shapefile to exclude saltwater bodies. Both layers were reclassified to obtain an area of 5 km (twice the maximum recorded terrestrial dispersal distance of *X. laevis;* Measey, 2016) around each grid cell containing water. For southern Africa, the layer was also reclassified to delimit an area of 200 km around each water grid cell, which was used as background-file for modelling. For modelling purposes we resampled each layer to 2.5 arcmin resolution. After modelling, we clipped the resulting SDM maps with the water-availability layers.

The species' records were randomly divided 100 times, with 70% used for model training and 30% used for model evaluation using a bootstrap approach. The Area Under the Receiver Operating Characteristic Curve (Swets, 1988) and True Skill Statistics (Allouche et al., 2006; Somodi et al., 2017) were used to evaluate model performance. We increased the number of maximum iterations from 500 to 5000 to give the model adequate time for convergence, although the model does not over- or under-predict relationships (Young et al., 2011). The average prediction across all 100 replicates was used as our final result. Distribution maps were displayed using Maxent's cloglog output format. "Minimum training presence cloglog threshold" was set as hypothetical thresholds for presence-absence (c.f. Phillips et al., 2006). MESS (Multivariate Environmental Similarity Surfaces) maps were provided to highlight possible extrapolation errors (Elith et al., 2010).

The *area*()-function of the *raster* package (Hijmans, 2016) was applied to predicted areas of the respective ranges, which were corrected by minimum training presence thresholds, to calculate the predicted areas of our SDMs and the correlative SDMs (Ihlow et al., 2016; Measey et al., 2012; Rödder et al., 2017). The results were rounded to 100 km^2 due to uncertainties in calculation. For calculation, the grid-files of the maps were reclassified with DIVA GIS (Hijmans et al., 2002). We set values above minimum training presence logistic/cloglog threshold as suitable area and reclassified them to get the value "1" while non-suitable area below this threshold was set as "NoData."

3 | RESULTS

3.1 | Ecophysiological performance surfaces

For adult frogs, the performance surfaces revealed significant effects of temperature on performance but very marginal effects of body size for all variables (Table 4). Performance surfaces of MaxVel for adult frogs revealed pred_perf = 2.8 m s^{-1}, T_{opt} = 29.1°C, CT_{min} = 2.8°C and CT_{max} = 35.1°C. The optimum body size to perform the best MaxVel was 72.2 mm. Both endurance variables revealed very low optimum temperatures. Critical thermal limits were similar to the other variables (EndurTime: native: pred_perf = 856.2 s, T_{opt} = 12.3°C, CT_{min} = 2.4°C, CT_{max} = 35.8°C, size = 78.0 mm; EndurDist: native: pred_perf = 35.9 m, T_{opt} = 19.0°C, CT_{min} = 2.9°C, CT_{max} = 36.8°C, size = 74.3 mm). EWL and SMR revealed nearly the same values for temperature and body size dependence (EWL: pred_perf = 0.4 mg h^{-1}, T_{opt} = 31.5°C, CT_{min} = 2.6°C, CT_{max} = 39.2°C, size = 51.5 mm; SMR: pred_perf = 12.3 ml h^{-1}, T_{opt} = 31.5°C, CT_{min} = 2.5°C, CT_{max} = 39.5°C, size = 52.1 mm).

For tadpoles, the performance surfaces of MaxVel and d200 revealed a similar pattern shown by the adult frogs (Table 4). Individuals of both rainfall regions show similar values for all categories of both locomotor variables (MaxVel: native_summerrain: pred_perf = 11.5 cm s^{-1}, T_{opt} = 30.2°C, CT_{min} = 3.2°C, CT_{max} = 38.6°C; native_winterrain: pred_perf = 12.2 cm s^{-1}, T_{opt} = 29.8°C, CT_{min} = 3.4°C, CT_{max} = 38.8°C; d200: native_summerrain: pred_perf = 1.5 cm, T_{opt} = 29.8°C, CT_{min} = 3.4°C, CT_{max} = 38.6°C; native_winterrain: pred_perf = 1.4 cm, T_{opt} = 29.3°C, CT_{min} = 3.7°C, CT_{max} = 39.3°C).

3.2 | Ecophysiological rasters

For adult frogs (Figure 1), the projections based on MaxVel showed a fragmented pattern for the native range with tendency of better performance in the north, while for the invasive range a gradient from western-coastal to eastern-continental (high to low values) is visible. Hours of activity for adult frogs are very high in nearly the

TABLE 4 Results for ecophysiological performance surfaces for adult and tadpole *Xenopus laevis*

	Performance	Pred_perf	Topt (°C)	CTmin (°C)	CTmax (°C)	Body size (mm)
Adult	MaxVel	2.8	29.1	2.8	35.1	72.2
	EndurTime	856.2	12.3	2.4	35.8	78.03
	EndurDist	35.9	19.0	2.9	36.8	74.3
	EWL	0.4	31.5	2.6	39.2	51.5
	SMR	12.3	31.5	2.5	39.5	52.1
Tadpoles Native SR	MaxVel	11.5	30.2	3.2	38.6	-
	d200	1.5	29.8	3.4	38.6	-
Tadpoles Native WR	MaxVel	12.2	29.8	3.4	38.8	-
	d200	1.4	29.3	3.7	39.3	-

Abbreviations: d200, distance moved in 200 ms; CTmin and CTmax, critical thermal limits; EndurDist, endurance; distance; EndurTime, endurance time; EWL, evaporative water loss; Pred_perf, predicted performance; MaxVel, optimal body size for the performance traits maximum velocity; SMR, standard metabolic rate; Topt, optimum temperature.

entire native range, while for the invasive range a western-coastal to eastern-continental gradient (high to low values) was found. The performance for hours of restriction was very low for both native and invasive range. The projections of EndurDist and EndurTime to the native and invasive range revealed a gradient from coast to inland (high to low values). Compared to EndurDist, EndurTime shows only small areas with high values. The projection of EWL and SMR to the native range revealed a north–south gradient (high to moderate values). The projection to the invasive range resulted in a moderate (western and southern Europe) to low (central-eastern Europe and mountain ranges) EWL performance.

All ecophysiological rasters for tadpoles (Figure 2) revealed similar patterns for summer and winter rainfall populations with no significant differences. For the native range, performance of MaxVel showed a north–south gradient (high to low values), while for the invasive range a gradient from western-coastal to eastern-continental (high to low values) was also found. The performance of d200 showed a uniform pattern in the entire native range, while for the invasive range a discrete pattern with low values in the mountain ranges (Alps, Pyrenees) and high values in the rest of Europe was found. Hours of activity were high in nearly the entire native range and showed a western-coastal to eastern-continental gradient (high to low values) in the invasive range. Hours of restriction were very low in both ranges.

3.3 | Species distribution modelling

Acknowledging the pairwise assessment of Spearman rank correlation coefficients between ecophysiological variables (Tables 2 and 3), the final set of predictors comprised MaxVel, hours of activity, hours of restriction, EndurTime and SMR for adult frogs, and MaxVel, hours of activity and hours of restriction all from summer rainfall region for tadpoles. EndurDist and EndurTime, EWL and SMR, as well as MaxVel, hours of activity and hours of restriction from summer rainfall region and their respective counterparts from winter rainfall region were highly correlated (rho > 0.75) and therefore constrained to the predictors EndurTime and SMR for adult frogs, and MaxVel, hours of activity and hours of restriction from summer rainfall region for tadpoles. D200 from both regions did not show specific geographical patterns, and was therefore omitted.

For adult frogs, SMR on average had the highest contribution across the 100 SDMs (72.9%), followed by EndurTime (23.3%), hours of activity (2%), MaxVel (0.9%) and hours of restriction (0.8%). Model performance was good ($AUC_{Training} = 0.775$, $AUC_{Test} = 0.768$, $TSS_{Training} = 0.904$, $TSS_{Test} = 0.901$). For tadpoles, MaxVel on average had the highest contribution across the 100 SDMs (87.2%), followed by hours of activity (12.7%), and hours of restriction (0.1%). Model performance was good ($AUC_{Training} = 0.733$, $AUC_{Test} = 0.727$, $TSS_{Training} = 0.801$, $TSS_{Test} = 0.796$). For adult frogs and tadpoles together, SMR on average had the highest contribution across the 100 SDMs (71.5%), followed by EndurTime (24.6%), hours of activity for adults (0.9%), hours of restriction for adults (0.7%), MaxVel of tadpoles (0.7%), MaxVel of adults (0.7%), hours of activity for tadpoles (0.6%) and hours of restriction for tadpoles (0.2%). Model performance was good ($AUC_{Training} = 0.777$, $AUC_{Test} = 0.766$, $TSS_{Training} = 0.900$, $TSS_{Test} = 0.896$). All SDMs predict similar patterns with suitable climate space for large parts of southern Africa as well as most of Europe (Figure 3). Large MESS areas are predicted in eastern Europe where predictions should be treated with caution.

Our approaches resulted in the largest area of predicted distribution for *X. laevis* with up to 1,949,900 km^2 in the European invasive range, while the correlative SDMs predicted much smaller distributions of 6.8%–51% (Table 5). For the native range, the combination model of adults and tadpoles also predicted the largest area among our ecophysiological SDMs (1,022,400 km^2), followed by the model for the adults (917,900 km^2), and last tadpoles (904,000 km^2). The correlative approaches predict 35.7%–169.9% of our maximum predicted area.

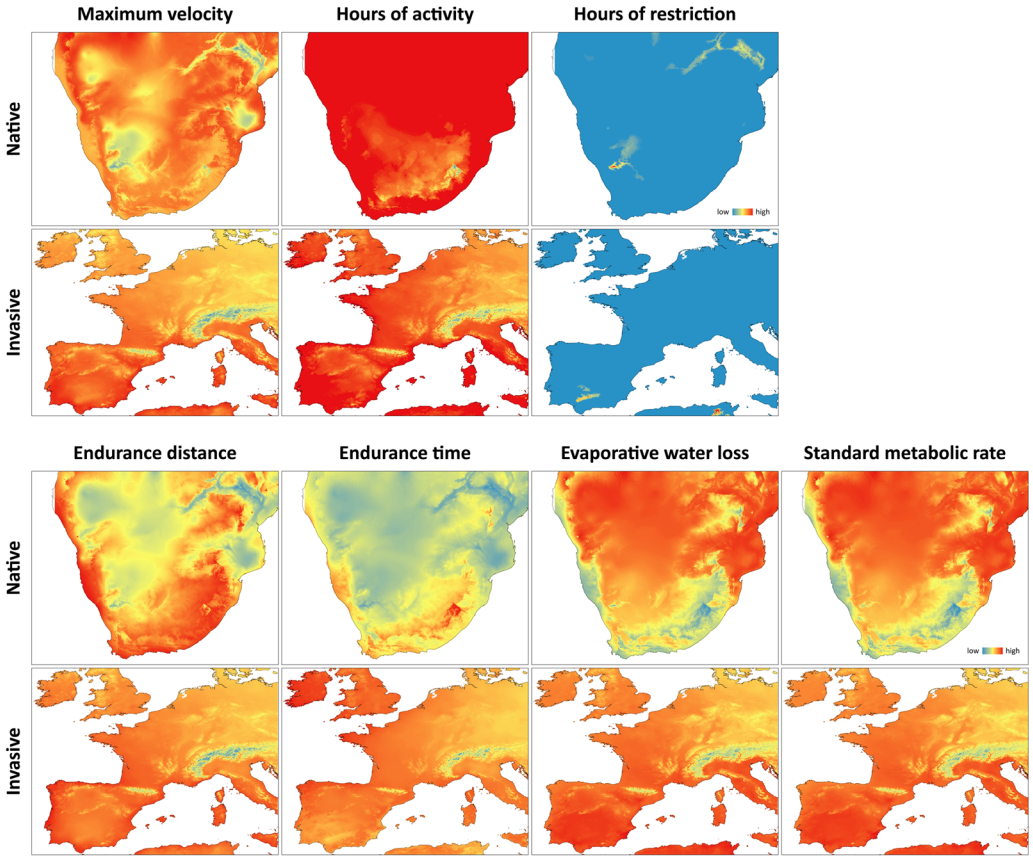

FIGURE 1 Ecophysiological rasters of adult *Xenopus laevis*: Performance assessed by maximum velocity (MaxVel), hours of activity, hours of restriction, endurance distance (EndurDist), endurance time (EndurTime), evaporative water loss (EWL), and standard metabolic rate (SMR) projected to the native and invasive range. Warm colors represent high values, while cold colors represent low values [Color figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

For adult frogs and tadpoles, the ecophysiological rasters revealed significant differences in locomotor performance, but similar patterns for hours of activity and hours of restriction (Figure 1+2). Our SDMs show that the physiological performance of adult frogs, especially SMR and EndurTime is the main driver for the predicted distributions. The locomotor performance of tadpoles had low variable contribution to the SDMs. Hours of activity and restrictions for adults and tadpoles and d200 of tadpoles seem to be not a significantly limiting factor for the potential distribution in Europe and southern Africa. The potential distribution suggested by the SDM matches the realized distribution of the species in southern Africa very well. Moreover, major parts of Europe are also characterized as suitable.

4.1 | Locomotor performance

Previous studies suggested that *X. laevis* preferred an ambient temperature of 22°C (Miller, 1982) and can withstand temperatures of 14°C to 32°C (Casterlin & Reynolds, 1980). Some authors assumed *X. laevis* can resist more extreme temperature limits (Nelson et al., 1982). The invasive population in France can withstand critical thermal limits from 2°C to 39°C (Courant & Herrel, personal communication). Laboratory studies indicate a different tolerance of extreme temperatures among the life stages (Balinsky, 1969; Wu & Gerhart, 1991) and ontogenetic shifts during embryonic development appear to affect thermal limits (Nelson et al., 1982). However, thermal tolerance data is limited to adult specimens originating from the Eastern Cape, but the temperature tolerances among the different native populations remains poorly studied (Rödder et al., 2017).

Our results support the observations that adult *X. laevis* can endure a broader temperature spectrum than previously assumed. T_{opt} for locomotor performance traits (MaxVel and d200) were similarly high among adults and tadpoles independent of summer or winter rainfall region (range: 29.1–30.2°C). While CT_{min} was similar among adults and tadpoles (range: 2.8–3.7°C), CT_{max} was much higher for tadpoles (range: 38.6–39.5°C) than for adults (35.1°C). Our results indicate that tadpoles can tolerate a broader temperature spectrum than previously suggested at least for short-term events. Although, it should be mentioned that it is challenging to conclude long-term performance and persistence in habitats from

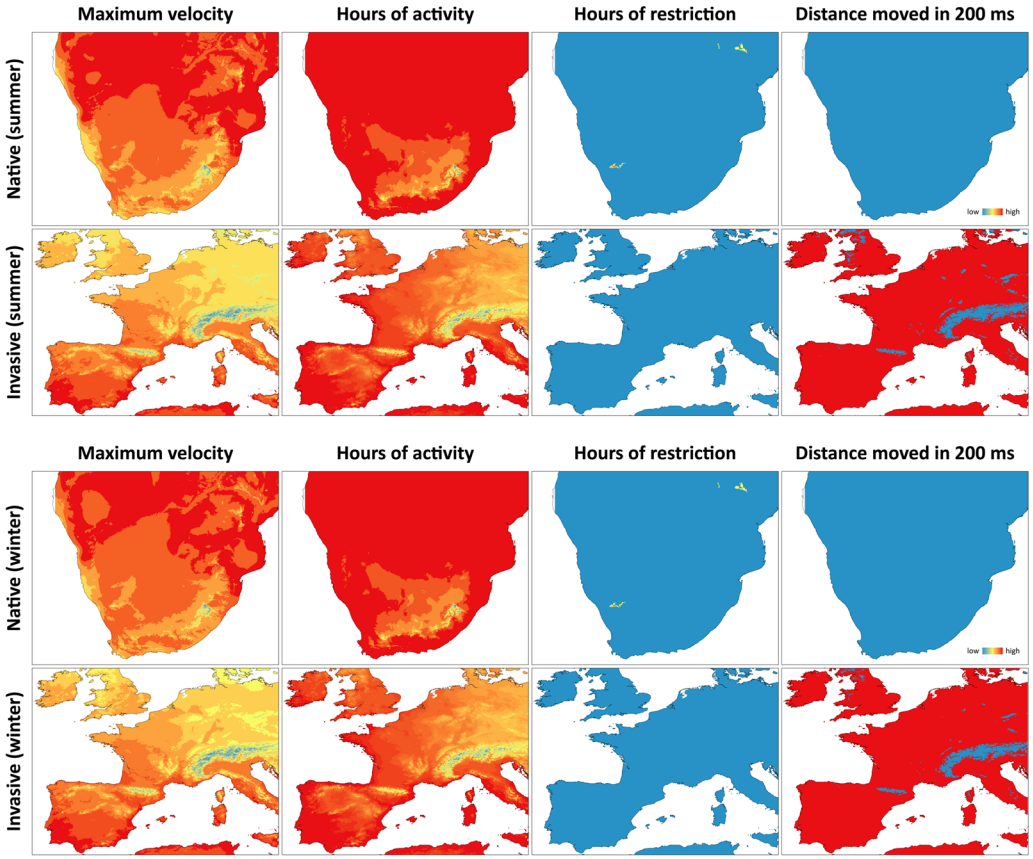

FIGURE 2 Ecophysiological rasters of tadpole *Xenopus laevis* from the summer (upper row) and winter rainfall region (lower row): Performance assessed by maximum velocity (MaxVel), distance moved in 200 ms (d200), hours of activity, and hours of restriction, projected to the native and invasive range. Warm colors represent high values, while cold colors represent low values [Color figure can be viewed at wileyonlinelibrary.com]

short-term experiments, and it remains unclear how the performance and critical thermal limits change when specimens are exposed to several hours, days or weeks of temperature extremes.

Southern Africa occupies a wide variety of biomes and bioregions from deserts, xeric shrubland, grasslands, Mediterranean forests to (sub-)tropical moist broadleaf forests (Rutherford et al., 2006; van Wilgen et al., 2020). The major parts of the distribution of the south-western Cape clade where most of the European populations were derived (De Busschere et al., 2016) is characterized by a Mediterranean climate (Measey et al., 2012): hot dry summers and cold wet winters. The species occurs in a wide geographic range from the winter rainfall regions in the south-western Cape to summer rainfall regions in the north, and from sea level up to 3000 m in Lesotho (Measey, 2004). According to the hours of activity and restriction the daily temperature variation in nearly all of the native range is suitable for the ecophysiological performance of *X. laevis*. The ecophysiological rasters show that the daily temperature extremes in southern Africa and Europe have only a marginal effect on the hours of restriction in both ranges.

The climate in western, central, southern and eastern Europe can be classified into three main climate types: Western Europe has an oceanic climate with mild winters and cool summers, eastern Europe provides a continental climate with cold winters and hot summers, whereas central Europe has a hybrid climate between these climates, and the Mediterranean sea region is characterized by mild, rainy winters and hot, dry summers. Especially the oceanic and Mediterranean regions of Europe seem suitable for new introductions of animals from native populations of *X. laevis*. The more eastern continental regions and mountain ranges (Alps, Pyrenees) seem unsuitable for the species, due to the temperature extremes. However, a recent study revealed that the French *X. laevis* population, which was introduced c. 40 years ago, went through a temperature dependant shift in their locomotor performance indicating a shift in the fundamental niche of the species. French animals are adapted to the colder European climate and endure a broader temperature spectrum than native individuals (Araspin et al., 2020).

4.2 | Physiological performance

Physiological variables such as EWL, SMR, EndurDist, and EndurTime give an indicator for energy use and balance, and are critical traits in

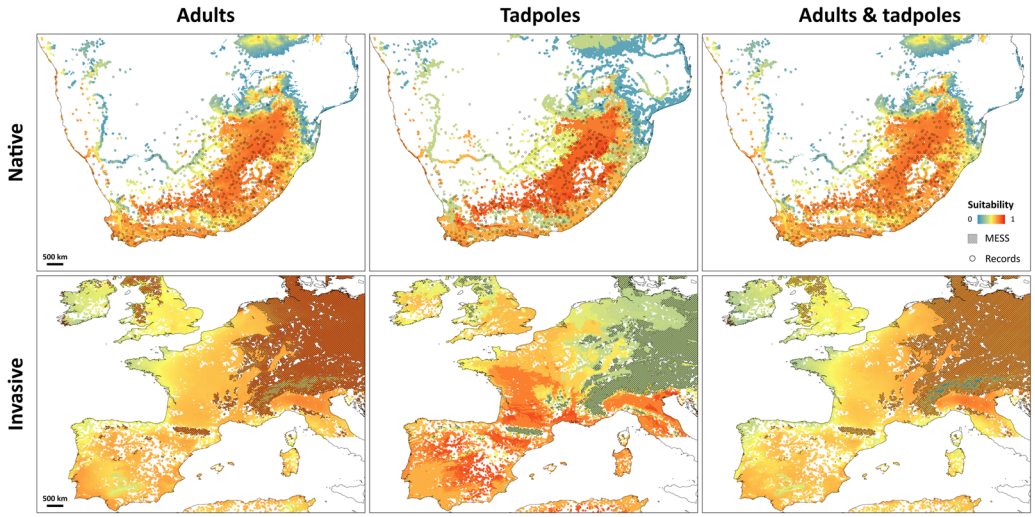

FIGURE 3 Ecophysiological models of adults, tadpoles and adults and tadpoles together based on data assessed from the native population projected to the native range (top) and the invasive European range (bottom). Dark colors represent highly suitable areas while light colors represent unsuitable areas. Dark gray areas represent MESS areas, which should be treated with caution because at least one predicting variable is exceeding the training range of the models and hence require extrapolation. Points represent the records [Color figure can be viewed at wileyonlinelibrary.com]

amphibian biology (Wygoda, 1984). However, for an aquatic species as *X. laevis* EWL is important during terrestrial movement only (Du Plessis, 1966; Measey & Tinsley, 1998; Mokhatla et al., 2019). Specimens from Great Britain are known to move up to 2 km a day (Measey & Tinsley, 1998). Capture-mark-recapture trials in the native region showed that *X. laevis* can move 2.36 km Euclidean distance on land, but mostly move between 200 and 400 m per dispersal event (De Villiers & Measey, 2017). Further, it is assumed that *X. laevis* uses small waterbodies during the rainy season to reach more distant locations (Faraone et al., 2008; Measey, 2016).

Our results show a gradient of SMR in the native range from north (high values) to south (low values) and one of EndurTime with highest values at the southern coast region. Despite this, the *X. laevis* extent of occurrence extends past the northern regions of South Africa (up to Malawi) with high predicted EWL and SMR. It seems more likely that the availability and density of waterbodies restricts the expansion of this species more than SMR, and it has been suggested that man-made impoundments have resulted in an expansion from a much more restricted original native range (Measey et al., 2017; Measey et al., 2020). Major parts of south-western to north-western regions of southern Africa are characterized by deserts and xeric savanna such as Kalahari, Succulent Karoo, Nama Karoo or Namib (Rutherford et al., 2006), where *X. laevis* is largely absent. Further, *X. laevis* has a broad tolerance spectrum of environmental conditions suffering a high anoxic tolerance (Measey et al., 2012) and can survive up to eight months without water, which is useful to survive droughts and to colonize ephemeral waterbodies (Tinsley & Kobel, 1996). The projection of EWL and SMR

TABLE 5 Comparison among our ecophysiological (Ginal et al., 2020) and previous correlative (Ihlow et al., 2016; Measey et al., 2012; Rödder et al., 2017) Species distribution model (SDM) approaches: Predicted area of distribution in the native and invasive range in km^2 and percentage relative to the ecophysiological SDM

	Native (km^2)	Native (%)	Invasive (km^2)	Invasive (%)
Ecophysiological SDM—Adults (Ginal et al., 2020)	917,900	89.8	1,949,900	100.0
Ecophysiological SDM—Tadpoles (Ginal et al., 2020)	904,000	88.4	1,949,900	100.0
Ecophysiological SDM—Adults and tadpoles (Ginal et al., 2020)	1,022,400	100.0	1,949,900	100.0
Maxent (Measey et al., 2012)	364,600	35.7	175,600	9.0
Maximum entropy (Ihlow et al., 2016)	908,300	88.8	803,200	41.2
Ensemble (Ihlow et al., 2016)	1,232,000	120.5	993,800	51.0
bdw approach (Rödder et al., 2017)	1,390,100	136.0	132,600	6.8
MCP approach (Rödder et al., 2017)	1,736,800	169.9	132,600	6.8

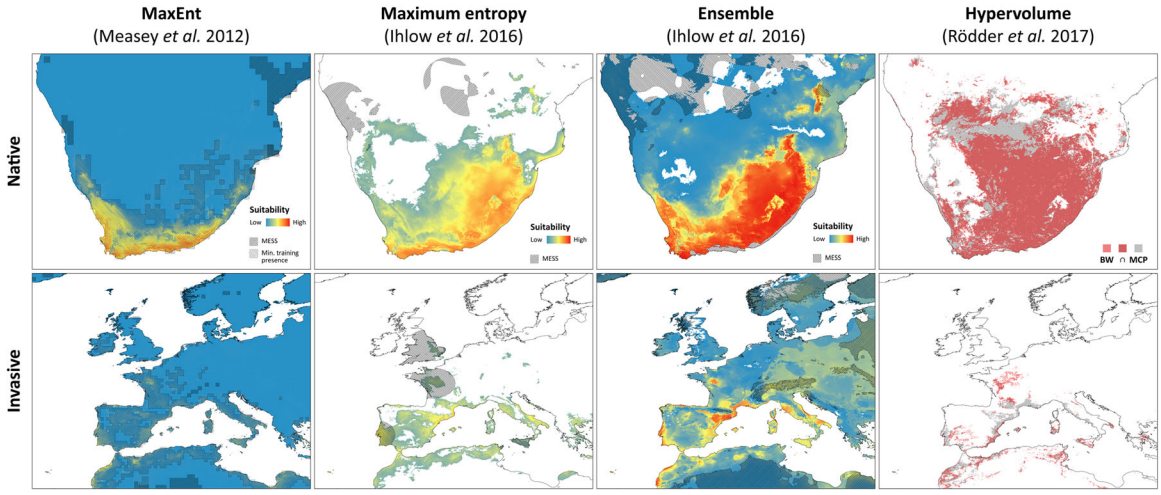

FIGURE 4 Comparison among different correlative SDM approaches from left to right: Maxent (Measey et al., 2012), maximum entropy and ensemble model (Ihlow et al., 2016), hypervolume models: bdw and mcp approach (Rödder et al., 2017). Minimum training presence was calculated as threshold (dark gray). The middle gray represents the area of extrapolation (MESS/MASK), which should be treated with caution because at least one predicting variable is exceeding the training range of the models and hence require extrapolation. The background is underplayed with a country layer (light gray) [Color figure can be viewed at wileyonlinelibrary.com]

performance onto Europe resulted in a west-east gradient (moderate to low values). Also a moderate to high EWL and SMR seems appropriate for a successful persistence of *X. laevis* because the currently colonized regions in Europe (Portugal, Rebelo et al., 2010; Sicily, Lillo et al., 2005) resemble the native, Mediterranean conditions most appropriate for the southwestern Cape clade population. Furthermore some of the invasive ranges, that is France (Fouquet, 2001), is characterized by a very high density of waterbodies, and a dense hydrographic network (Vimercati et al., 2020) which suggests that pressures regarding water losses are much milder than in the native range (compare to Figure 3 and see Section 2 for background selection). However, two invasive populations persisted for decades in Great Britain and also reproduced (Measey, 2001), where a moderate EWL and SMR is predicted. It was speculated that their disappearance was linked to extreme weather conditions (cold and drought) of consecutive winters, suggesting climatic conditions surpassed the buffering capacity of the microhabitat (Tinsley et al., 2015). The second key driver of *X. laevis* distribution is EndurTime which is highest in regions with moderate climate.

The combination of SMR and EndurTime of adult frogs seem to be the best predicting variables for *X. laevis* distribution with highest contribution to the 100 SDMs (SMR: 72.9% for adults and 71.5% for adults and tadpoles combined; EndurTime: 23.3% for adults and 24.6% for adults and tadpoles combined).

4.3 | Comparison among correlative and physiological SDMs

In contrast to previous correlative SDMs (Ihlow et al., 2016; Measey et al., 2012; Rödder et al., 2017), our work reveals a much higher risk of invasion, especially for most parts of Europe (compare to Table 5, Figures 3 and 4). The ecophysiological SDMs for adult frogs, tadpoles, and both life stages combined revealed similar patterns for the native range and an almost identical pattern for the invasive range, although the SDM taking into account adults and tadpoles together revealed the largest predicted area for the native range. For the native range, particularly southern to eastern southern Africa is predicted as suitable habitat, while the deserts and xeric savanna in the south-western to north-western regions are climatically unsuitable. Cold areas such as mountain ranges like Drakensberg are predicted as mostly unsuitable, despite the known presence of this species there (Measey, 2004). It is possible that the specimens from these regions locally adapted to a much colder high-altitudinal environment. For the invasive European range, especially large parts of western, southern and central Europe as well as large parts of the North African coastline and many Mediterranean islands are predicted as being climatically suitable for *X. laevis*. This also includes the currently occupied areas Portugal, France, and Wales, while Sicily is predicted as unsuitable, which is probably due to the low density of waterbodies, which is probably as this area could not be assessed by our waterbody availability layer. Further, large MESS areas in central to eastern Europe as well as cold mountain ranges such as Alps and Pyrenees are predicted, where predictions should be treated with caution.

The assessment of physiological limits indicates that *X. laevis* is a species with high potential to acclimatize to novel environmental conditions that can survive temperature extremes and shows a broad temperature spectrum, allowing it to colonize even temperate regions in Europe. Further, temperature in microhabitats can deviate strongly from those of the wider ecosystems, effectively buffering extremes and therefore reducing mortality rates during extreme weather events (Scheffers et al., 2014). On larger time scales, like monthly averages, the buffering capacity may be reduced as the averages of the microhabitat temperature and ambient temperature may reach equilibrium (Rödder et al., 2017). Water, the principle habitat of *X. laevis*, buffers short-term

weather extremes of air temperature and provides shelter during these events (Lampert & Sommer, 2007). In lentic habitats, water temperatures in the hypolimnion do not decrease below 4°C (Lampert & Sommer, 2007), effectively protecting submerged frogs from potentially lethal minimum air temperatures. It is known that specimens avoid exposure to critical temperatures by moving into cooler water sections when exposed to high temperatures (47°C) in Arizona (Measey, 1997) or dig pits into the mud (McCoid & Fritts, 1980). Freezing may be a major mortality factor (Eggert & Fouquet, 2006), although specimens were observed moving at 5°C (Wilson et al., 2000) and throughout winter in France (Courant & Herrel, personal communication) and swimming under ice in Wales (Measey, 2001). While adult frogs may be active and foraging under ice-covered water, the development of tadpoles is hampered under these conditions (Measey, 1997).

5 | CONCLUSION

According to our ecophysiological SDMs, *X. laevis* has a much higher invasive potential than previous correlative approaches had suggested. An area of 1,949,900 km^2 is predicted as potentially climatically suitable for *X. laevis*. Especially the oceanic and Mediterranean climate spaces in Europe and North Africa seem to be an ideal habitat. Additionally, an ongoing shift in the fundamental niche of the French population combined with scenarios of climate change could lead to further expansion into new ranges, which are currently predicted to be unsuitable for this species. The French invasive population seems to make use of hydrographic networks and has now reached the Loire River catchment which covers about 20% of the French national territory. River networks may assist the expansion even in areas with moderately suitable conditions. Moreover, the establishment of new populations through release or escape is quite likely. For this reason, further knowledge about expansion pathways and concrete management efforts are necessary to halt the spread or eradicate this high-risk invasive species.

ACKNOWLEDGMENTS

This study was funded by an ERA-Net BiodivERsA grant INVAXEN, with the national funders ANR, DFG (RO 4520/3-1), BELSPO and FCT, as part of the 2013 BiodivERsA call for research proposals. Natasha Kruger, Mohlamatsane Mokhatla and John Measey would like to thank the DSI-NRF Centre of Excellence for Invasion Biology (South Africa). Natasha Kruger would like to acknowledge the Ambassade de France en Afrique du Sud (France). Dennis Rödder and Philipp Ginal are grateful to B. Sinervo for sharing his experience and R scripts during a workshop held at the World Congress of Herpetology in Tonglu, China. Ursula Bott helped with her excellent proof reading skills.

CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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REFERENCES

Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, *43*(6), 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x

Angilletta, M. J., Niewiarowski, P. H., & Navas, C. A. (2002). The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology*, *27*, 249–268. https://doi.org/10.1016/S0306-4565(01)00094-8

Araspin, L., Martinez, A. S., Wagener, C., Courant, J., Louppe, V., Padilla, P., Measey, J., & Herrel, A. (2020). Rapid shifts in the temperature dependence of locomotor performance in an invasive frog, *Xenopus laevis*, implications for conservations. *Integrative and Comparative Biology*, *60*, 456–466. https://doi.org/10.1093/icb/icaa010

Balinsky, B. I. (1969). The reproductive ecology of amphibians of the Transvaal highveld. *Zoologica Africana*, *4*(1), 37–93.

Bennet, A. F. (1990). Thermal dependence of locomotor capacity. *The American Physiological Society*, *259*, R253–R258.

Blaustein, A. R., Han, B. A., Relyea, R. A., Johnson, P. T. J., Buck, J. C., Gervasi, S. S., & Kats, L. B. (2011). The complexity of amphibian population declines: Understanding the role of cofactors in driving amphibian losses. *Year in Ecology and Conservation Biology*, *1223*, 108–119. https://doi.org/10.1111/j.1749-6632.2010.05909.x

Broennimann, O., Treier, U. A., Müller-Schärer, H., Thuiller, W., Peterson, A. T., & Guisan, A. (2007). Evidence of climatic niche shift during biological invasion. *Ecology Letters*, *10*, 701–709. https://doi.org/10.1111/j.1461-0248.2007.01060.x

Brown, D. (2009). Video modelling with tracker. American Association of Physics Teachers (AAPT), Summer Meeting (Ann Arbor).

Buckley, L. B. (2008). Linking traits to energetics and population dynamics to predict lizard ranges in changing environments. *American Naturalist*, *171*(1), E1–E19. https://doi.org/10.1086/523949

Buckley, L. B., Waaser, S. A., MacLean, H. J., & Fox, R. (2011). Does including physiology improve species distribution model predictions of responses to recent climate change? *Ecology*, *92*(12), 2214–2221. https://doi.org/10.1890/11-0066.1

Case, M. J., & Lawler, J. J. (2017). Integrating mechanistic and empirical model projections to assess climate impacts on tree species distributions in northwestern North America. *Global Change Biology*, *23*(5), 2005–2015. https://doi.org/10.1111/gcb.13570

Casterlin, M. E., & Reynolds, W. W. (1980). Diel activity and thermoregulatory behavior of a fully aquatic frog—*Xenopus laevis*. *Hydrobiologia*, *75*(2), 189–191. https://doi.org/10.1007/Bf00007433

Ceia-Hasse, A., Sinervo, B., Vicente, L., & Pereira, H. M. (2014). Integrating ecophysiological models into species distribution projections of European reptile range shifts in response to climate change. *Ecography*, *37*(7), 679–688. https://doi.org/10.1111/j.1600-0587.2013.00600.x

Courant, J., Secondi, J., Vollette, J., Herrel, A., & Thirion, J. M. (2018). Assessing the impacts of the invasive frog, *Xenopus laevis*, on amphibians in western France. *Amphibia-Reptilia*, *39*(2), 219–227.

Courant, J., Vogt, S., Marques, R., Measey, J., Secondi, J., Rebelo, R., De Villiers, A., Ihlow, F., De Buschere, C., Backeljau, T., Rödder, D., & Herrel, A. (2017). Are invasive populations characterized by a broader diet than native populations? *PeerJ*, *5*, e3250. https://doi.org/10.7717/peerj.3250

Courant, J., Vollette, E., & Herrel, A. (2018). Changes in the aquatic macro-invertebrate communities through the expanding range of an invasive anuran. *Food Webs*, *17*, e00098.

De Busschere, C., Courant, J., Herrel, A., Rebelo, R., Rödder, D., Measey, G. J., & Backeljau, T. (2016). Unequal contribution of native South African phylogeographic lineages to the invasion of the African clawed frog, *Xenopus laevis*, in Europe. *PeerJ*, *4*, e1659. https://doi.org/10.7717/peerj.1659

De Villiers, F. A., & Measey, J. (2017). Overland movement in African Clawed Frogs (*Xenopus laevis*): Empirical dispersal data from within their native range. *PeerJ*, *5*, e4039.

Dudik, M., Philips, S. J., & Shapire, R. E. (2004). A maximum entropy approach to species distribution modelling. In *Proceedings of the 21st international conference on machine learning*.

Du Plessis, S. S. (1966). Stimulation of spawning in *Xenopus laevis* by fowl manure. *Nature*, *211*, 1092.

Dunlap, D. G. (1971). Acutely measured metabolic rate—Temperature curves in the Cricket Frog *Acris crepitans*. *Comparative Biochemistry and Physiology—Part A: Molecular & Integrative Physiology*, *38*, 1–16.

Eggert, C., & Fouquet, A. (2006). A preliminary biotelemetric study of a ferai invasive *Xenopus laevis* population in France. *Alytes*, *23*, 144–149.

Elith, J., Kearney, M., & Phillips, S. (2010). The art of modelling range-shifting species. *Methods in Ecology and Evolution*, *1*(4), 330–342. https://doi.org/10.1111/j.2041-210X.2010.00036.x

Elith, J., Phillips, S. J., Hastie, T., Dudik, M., Chee, Y. E., & Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, *17*(1), 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x

ESRI. (2008). ArcMap v. 9.2. *ESRI*.

Faraone, F. P., Lillo, F., Giacalone, G., & Lo Valvo, M. (2008). The large invasive population of *Xenopus laevis* in Sicily, Italy. *Amphibia-Reptilia*, *29*(3), 405–412. https://doi.org/10.1163/156853808785112075

Feder, M. E., & Burggren, W. W. (1992). *Environmental physiology of the amphibians*. University of Chicago Press.

Ficetola, G. F., Maiorano, L., Falcucci, A., Dendoncker, N., Boitani, L., Padoa-Schioppa, E., & Thuiller, W. (2010). Knowing the past to predict the future: Land-use change and the distribution of invasive bullfrogs. *Global Change Biology*, *16*(2), 528–537. https://doi.org/10.1111/j.1365-2486.2009.01957.x

Ficetola, G. F., Thuiller, W., & Miaud, C. (2007). Prediction and validation of the potential global distribution of a problematic alien invasive species—The American bullfrog. *Diversity and Distributions*, *13*, 476–485. https://doi.org/10.1111/j.1472-4642.2007.00377.x

Fouquet, A. (2001). Des clandestins aquatiques. *Zamenis*, *6*, 10–11.

Gilman, S. E., Wethey, D. S., & Helmuth, B. (2006). Variation in the sensitivity of organismal body temperature to climate change over local and geographic scales. *Proceedings of the National Academy of Science USA*, *103*(25), 9560–9565. https://doi.org/10.1073/pnas.0510992103

Gonzalez-del-Pliego, P., Freckleton, R. P., Edwards, D. P., Koo, M. S., Scheffers, B. R., Pyron, R. A., & Jetz, W. (2019). Phylogenetic and trait-based prediction of extinction risk for data-deficient amphibians. *Current Biology*, *29*(9), 1557–1563. https://doi.org/10.1016/j.cub.2019.04.005

Grinnell, J. (1917). The niche-relationships of the California Thrasher. *Auk*, *34*, 427–433.

Gurdon, J. B., & Hopwood, N. (2003). The introduction of *Xenopus laevis* into developmental biology: Of empire, pregnancy testing and ribosomal genes. *International Journal of Developmental Biology*, *44*(1), 43–50.

Herrel, A., & Bonneaud, C. (2012a). Temperature dependence of locomotor performance in the tropical clawed frog, *Xenopus tropicalis*. *Journal of Experimental Biology*, *215*(14), 2465–2470. https://doi.org/10.1242/jeb.069765

Herrel, A., & Bonneaud, C. (2012b). Trade-offs between burst performance and maximal exertion capacity in a wild amphibian, *Xenopus tropicalis*. *Journal of Experimental Biology*, *215*(17), 3106–3111. https://doi.org/10.1242/jeb.072090

Herrel, A., Gonwouo, L. N., Fokam, E. B., Ngundu, W. I., & Bonneaud, C. (2012). Intersexual differences in body shape and locomotor performance in the aquatic frog, *Xenopus tropicalis*. *Journal of Zoology*, *287*(4), 311–316. https://doi.org/10.1111/j.1469-7998.2012.00919.x

Herrel, A., & van der Meijden, A. (2014). An analysis of the live reptile and amphibian trade in the USA compared to the global trade in endangered species. *Herpetological Journal*, *24*(2), 103–110.

Herrel, A., Vasilopoulou-Kampitsi, M., & Bonneaud, C. (2014). Jumping performance in the highly aquatic frog, *Xenopus tropicalis*: Sex-specific relationships between morphology and performance. *PeerJ*, *2*, e661. https://doi.org/10.7717/peerj.661

Hijmans, R. J. (2016). Raster: Geographic data analysis and modeling. R package version 2.5-8. https://CRAN.R-project.org/package=raster

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, *25*, 1965–1978. https://doi.org/10.1002/joc.1276

Hijmans, R. J., Guarino, L., & Rojas, E. (2002). *DIVA-GIS*. A geographic information system for the analysis of biodiversity data. Manual. International Potato Center.

Huey, R. B., & Kingsolver, J. G. (1989). Evolution of thermal sensitivity of ectotherm performance. *Trends in Ecology and Evolution*, *4*, 131–135.

Hutchinson, G. E. (1978). *An introduction to population ecology*. Yale Universtity Press.

Huey, R. B., Losos, J. B., & Moritz, C. (2010). Are lizards toast? *Science*, *328*(5980), 832–833. https://doi.org/10.1126/science.1190374

Ihlow, F., Courant, J., Secondi, J., Herrel, A., Rebelo, R., Measey, J., Lillo, F., De Villiers, F. A., Vogt, S., De Busschere, C., Backeljau, T., & Rödder, D. (2016). Impacts of climate change on the global invasion potential of the African clawed frog *Xenopus laevis*. *PLOS One*, *11*(6): e0154869. https://doi.org/10.1371/journal.pone.0154869

James, R. S., Tallis, J., Herrel, A., & Bonneaud, C. (2012). Warmer is better: Thermal sensitivity of both maximal and sustained power output in the iliotibialis muscle isolated from adult *Xenopus tropicalis*. *Journal of Experimental Biology*, *215*(3), 552–558. https://doi.org/10.1242/jeb.063396

Jimenez-Valverde, A., Peterson, A. T., Soberon, J., Overton, J. M., Aragon, P., & Lobo, J. M. (2011). Use of niche models in invasive species risk assessments. *Biological Invasions*, *13*(12), 2785–2797. https://doi.org/10.1007/s10530-011-9963-4

Kearney, M., Phillips, B. L., Tracy, C. R., Christian, K. A., Betts, G., & Porter, W. P. (2008). Modelling species distributions without using species distributions: The cane toad in Australia under current and future climates. *Ecography*, *31*(4), 423–434. https://doi.org/10.1111/j.0906-7590.2008.05457.x

Kearney, M., & Porter, W. (2009). Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. *Ecology Letters*, *12*(4), 334–350. https://doi.org/10.1111/j.1461-0248.2008.01277.x

Kearney, M., & Porter, W. P. (2004). Mapping the fundamental niche: Physiology, climate, and the distribution of a nocturnal lizard. *Ecology*, *85*(11), 3119–3131. https://doi.org/10.1890/03-0820

Kolbe, J. J., Kearney, M., & Shine, R. (2010). Modeling the consequences of thermal trait variation for the cane toad invasion of Australia. *Ecological Applications*, *20*(8), 2273–2285. https://doi.org/10.1890/09-1973.1

Lafferty, K. D., & Page, C. J. (1997). Predation on the endangered tidewater goby, *Eucyclogobius newberryi*, by the introduced African clawed frog, *Xenopus laevis*, with notes on the frog's parasites. *Copeia*, *3*, 589–592. https://doi.org/10.2307/1447564

Lampert, W., & Sommer, U. (2007). *Limnoecology—The ecology of lakes and streams*. Oxford University Press.

Lighton, J. R. (2008). Measuring metabolic rates of: A manual for scientists.

Lillo, F., Marrone, F., Sicilia, A., Castelli, G., & Zava, B. (2005). An invasive population of *Xenopus laevis* (Daudin, 1802) in Italy. *Herpetozoa*, *18*, 63–64.

McCoid, M. J., & Fritts, T. H. (1980). Observations of feral populations of *Xenopus laevis* (Pipidae) in southern California. *Bulletin of the Southern California Academy of Sciences*, *79*, 82–86.

McCoid, M. J., & Fritts, T. H. (1989). Growth and fat-body cycles in feral populations of the African Clawed Frog, *Xenopus laevis* (Pipidae), in California with comments on reproduction. *Southwestern Naturalist*, *34*(4), 499–505. https://doi.org/10.2307/3671508

Measey, J. (1997). Ecology of feral *Xenopus* (Ph.D. dissertation, University of Bristol).

Measey, J. (2001). Growth and ageing of feral *Xenopus laevis* (Daudin) in South Wales, UK. *Journal of Zoology*, *254*, 547–555. https://doi.org/10.1017/S0952836901001054

Measey, J. (2004). Species account: *Xenopus laevis*. In L. R. Minter, M. Burger, J. A. Harrison, H. H. Braak, & P. J. Bishop (Eds.), *Atlas and red data book of the frogs of South Africa, Lesotho and Swaziland*. Smithsonian Institution Press.

Measey, J. (2016). Overland movement in African clawed frogs (*Xenopus laevis*): A systematic review. *PeerJ*, *4*(9), e2474. https://doi.org/10.7717/peerj.2474

Measey, J. (2017). Where do African clawed frogs come from? An analysis of trade in live *Xenopus laevis* imported into the USA. *Salamandra*, *53*(3), 398–404.

Measey, J., Davies, S. J., Vimercati, G., Rebelo, A., Schmidt, W., & Turner, A. (2017). Invasive amphibians in southern Africa: A review of invasion pathways. *Bothalia*, *47*(2), a2117. https://doi.org/10.4102/abc.v47i2.2117

Measey, J., Hui, C., & Somers, M. J. (2020). Terrestrial vertebrate invasions in South Africa. In B. van Wilgen, J. Measey, D. Richardson, J. Wilson, & T. Zengeya (Eds.), *Biological invasions in South Africa. Invading nature.* Springer Series in Invasion Ecology (Vol. 14). Springer.

Measey, J., Robinson, T. B., Kruger, N., Zengeya, T. A., & Hurley, B. P. (2020). South Africa as a donor of alien animals. In B. van Wilgen, J. Measey, D. Richardson, J. Wilson, & T. Zengeya (Eds.), Biological invasions in South Africa. Invading nature. Springer Series in Invasion Ecology (Vol. 14). Springer.

Measey, J., Rödder, D., Green, S. L., Kobayashi, R., Lillo, F., Lobos, G., Rebelo, R., & Thirion, J.-M. (2012). Ongoing invasions of the African clawed frog, *Xenopus laevis*: A global review. *Biological Invasions*, *14*(11), 2255–2270. https://doi.org/10.1007/s10530-012-0227-8

Measey, J., & Tinsley, R. C. (1998). Feral *Xenopus laevis* in South Wales. *Herpetological Journal*, *8*, 23–27.

Measey, J., Vimercati, G., de Villiers, F. A., Mokhatla, M., Davies, S. J., Thorp, C. J., Rebelo, A. D., & Kumschick, S. (2016). A global assessment of alien amphibian impacts in a formal framework. *Diversity and Distributions*, *22*(9), 970–981. https://doi.org/10.1111/ddi.12462

Miller, D., Summers, J., & Silber, S. (2004). Environmental versus genetic sex determination: A possible factor in dinosaur extinction? *Fertility and Sterility*, *81*(4), 954–964. https://doi.org/10.1016/j.fertnstert.2003.09.051

Miller, K. (1982). Effect of temperature on sprint performance in the frog *Xenopus laevis* and the salamander *Necturus maculosus*. *Copeia*, *1982*(3), 695–698. https://doi.org/10.2307/1444671

Mokhatla, M., Measey, J., & Smit, B. (2019). The role of ambient temperature and body mass on body temperature, standard metabolic rate and evaporative water loss in southern African anurans of different habitat specialisation. *PeerJ*, *7*, e7885. ARTN. https://doi.org/10.7717/peerj.7885

Molkenthin, M. Retrieved from http://www.europakarte.org/

Morin, X., & Thuiller, W. (2009). Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology*, *90*(5), 1301–1313. https://doi.org/10.1890/08-0134.1

Navas, C. A. (1996). Metabolic physiology, locomotor performance, and thermal niche breadth in neotropical anurans. *Physiological Zoology*, *69*(6), 1481–1501. https://doi.org/10.1086/physzool.69.6.30164271

Nelson, L., Mild, K. H., & Lovtrup, S. (1982). Changes in temperature tolerance during the development of *Xenopus laevis* embryos. *Journal of Experimental Zoology*, *222*(1), 103–104. https://doi.org/10.1002/jez.1402220114

Nieuwkoop, P. D., & Faber, J. (1994). Normal table of *Xenopus laevis* (Daudin): A systematical and chronological survey of the development from the fertilized egg till the end of metamorposis. Routledge, ISBN 0815318960.

Nori, J., Urbina-Cardona, J. N., Loyola, R. D., Lescano, J. N., & Leynaud, G. C. (2011). Climate change and American bullfrog invasion: What could we expect in South America? *PLOS One*, *6*(10): e25718. https://doi.org/10.1371/journal.pone.0025718

Nunes, A. L., Fill, J. M., Davies, S. J., Louw, M., Rebelo, A. D., Thorp, C. J., Vimercanti, G., & Measey, J. (2019). A global meta-analysis of the ecological impacts of alien species on native amphibians. *Proceedings of the Royal Society B. 286*, 2018–2528. https://doi.org/10.1098/rspb.2018.2528

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*(6918), 37–42. https://doi.org/10.1038/nature01286

Pekel, J. F., Cottam, A., Gorelick, N., & Belward, A. S. (2016). High-resolution mapping of global surface water and its long-term changes. *Nature*, *540*(7633), 418–422. https://doi.org/10.1038/nature20584

Peterson, A. T., Papes, M., & Soberón, J. (2015). Mechanistic and correlative models of ecological niches. *European Journal of Ecology*, *1*(2), 28–38. https://doi.org/10.1515/eje-2015-0014

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*, 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

QGIS Team. (2020). QGIS Geographic Information System. Open Source Geospatial Foundation Project. Retrieved from http://qgis.osgeo.org

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Rago, A., While, G. M., & Uller, T. (2012). Introduction pathway and climate trump ecology and life history as predictors of establishment success in alien frogs and toads. *Ecology and Evolution*, *2*(7), 1437–1445. https://doi.org/10.1002/ece3.261

Rebelo, R., Amaral, P., Bernardes, M., Oliveira, J., Pinheiro, P., & Leitao, D. (2010). *Xenopus laevis* (Daudin, 1802), a new exotic amphibian in Portugal. *Biological Invasions*, *12*(10), 3383–3387. https://doi.org/10.1007/s10530-010-9757-0

Rutherford, M. C., Mucina, L., & Powrie, L. W. (2006). Biomes and bioregions of southern Africa. *Strelizia*, *19*.

Rödder, D., Ihlow, F., Courant, J., Secondi, J., Herrel, A., Rebelo, R., Measey, J., Lillo, F., De Villiers, F. A., De Busschere, C., & Backeljau, T. (2017). Global realized niche divergence in the African clawed frog *Xenopus laevis*. *Ecology and Evolution*, *7*(11), 4044–4058. https://doi.org/10.1002/ece3.3010

Scheffers, B. R., Edwards, D. P., Diesmos, A., Williams, S. E., & Evans, T. A. (2014). Microhabitats reduce animal's exposure to climate extremes. *Global Change Biology*, *20*(2), 495–503. https://doi.org/10.1111/gcb.12439

Sinclair, B. J., Stinziano, J. R., Williams, C. M., MacMillan, H. A., Marshall, K. E., & Storey, K. B. (2013). Real-time measurement of metabolic rate during freezing and thawing of the wood frog, *Rana sylvatica*: Implications for overwinter energy use. *Journal of Experimental Biology*, *216*(2), 292–302. https://doi.org/10.1242/jeb.076331

Sinervo, B., Mendez-de-la-Cruz, F., Miles, D. B., Heulin, B., Bastiaans, E., Cruz, M. V. S., Lara-Resendiz, R., Martinez-Mendez, N., Galderon-Espinosa, M. L., Meza, R., Gadsden, H., Avilar, L. J., Morando, M., De la Riva, I. J., Sepulveda, pV., Duarte Rocha, C. F., Ibargüengoytia, N., Puntriano, C. A., Massot, M., … Sites, J. W. (2010). Erosion of lizard diversity by climate change and altered thermal niches. *Science*, *328*(5980), 894–899. https://doi.org/10.1126/science.1184695

Soberón, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, *10*, 1115–1123.

Soberón, J., & Peterson, A. T. (2005). Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics*, *2*, 1–10.

Solis, R., Lobos, G., Walker, S. F., Fisher, M., & Bosch, J. (2010). Presence of *Batrachochytrium dendrobatidis* in feral populations of *Xenopus laevis* in Chile. *Biological Invasions*, *12*(6), 1641–1646. https://doi.org/10.1007/s10530-009-9577-2

Somodi, I., Lepesi, N., & Botta-Dukat, Z. (2017). Prevalence dependence in model goodness measures with special emphasis on true skill statistics. *Ecology and Evolution*, *7*(3), 863–872. https://doi.org/10.1002/ece3.2654

Steyermark, A. C., Miamen, A. G., Feghahati, H. S., & Lewno, A. W. (2005). Physiological and morphological correlates of among-individual variation in standard metabolic rate in the leopard frog *Rana pipiens*. *Journal of Experimental Biology*, *208*(6), 1201–1208. https://doi.org/10.1242/jeb.01492

Swets, J. A. (1988). Measuring the accuracy of diagnostic systems. *Science*, *240*(4857), 1285–1293.

Tejedo, M., & Reques, R. (1994). Plasticity in metamorphic traits of Natterjack tadpoles—The interactive effects of density and pond duration. *Oikos*, *71*(2), 295–304. https://doi.org/10.2307/3546278

Thuiller, W. (2007). Biodiversity—Climate change and the ecologist. *Nature*, *448*(7153), 550–552. https://doi.org/10.1038/448550a

Thuiller, W., Araujo, M. B., & Lavorel, S. (2004). Do we need land-cover data to model species distributions in Europe? *Journal of Biogeography*, *31*(3), 353–361. https://doi.org/10.1046/j.0305-0270.2003.00991.x

Tingley, R., Romagosa, C. M., Kraus, F., Bickford, D., Phillips, B. L., & Shine, R. (2010). The frog filter: Amphibian introduction bias driven by taxonomy, body size and biogeography. *Global Ecology and Biogeography*, *19*(4), 496–503.

Tinsley, R.C., & Kobel, H.R. (1996). The biology of Xenopus, London: Zoological Society of London.

Tinsley, R. C., Stott, L. C., Viney, M. E., Mable, B. K., & Tinsley, M. C. (2015). Extinction of an introduced warm-climate alien species, *Xenopus laevis*, by extreme weather events. *Biological Invasions*, *17*(11), 3183–3195. https://doi.org/10.1007/s10530-015-0944-x

van Sittert, L., & Measey, G. J. (2016). Historical perspectives on global exports and research on African clawed frogs (*Xenopus laevis*). *Transactions of the Royal Society of South Africa*, *71*, 157–166. van. https://doi.org/10.1080/0035919X.2016.1158747

van Wilgen, B. W., Measey, J., Richardson, D. M., Wilson, J. R., & Zengeya, T. A. (2020). Biological invasions in South Africa: On overview. In B. van Wilgen, J. Measey, D. Richardson, J. Wilson, & T. Zengeya (Eds.), *Invading nature*. Springer Series in Invasion Ecology. Springer.

van Wilgen, N. J., Gillespie, M. S., Richardson, D. M., & Measey, J. (2018). A taxonomically and geographically constrained information base limits non-native reptile and amphibian risk assessment: A systematic review. *PeerJ*, *6*, e5850. https://doi.org/10.7717/peerj.5850

Vimercati, G., Labadesse, M., Dejean, T., & Secondi, J. (2020). Assessing the effect of landscape features on pond colonisation by an elusive amphibian invader using environmental DNA. *Freshwater Biology*, *65*(3), 502–513.

Vogt, S., Villiers, F. A., Ihlow, F., Rödder, D., & Measey, J. (2017). Competition and feeding ecology in two sympatric *Xenopus* species (Anura: Pipidae). *PeerJ*, *5*, e3130 de. https://doi.org/10.7717/peerj.3130

Wake, D. B., & Vredenburg, V. T. (2008). Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proceedings of the National Academy of Science USA*, *105*, 11466–11473. https://doi.org/10.1073/pnas.0801921105

Wang, S., Hong, Y., & Measey, J. (2019). An established population of African clawed frogs, *Xenopus laevis* (Daudin, 1802), in mainland China. *BioInvasions Records*, *8*(2), 457–464. https://doi.org/10.3391/bir.2019.8.2.29

Wilson, R. S., James, R. S., & Johnston, I. A. (2000). Thermal acclimation of locomotor performance in tadpoles and adults of the aquatic frog *Xenopus laevis*. *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology*, *170*(2), 117–124. https://doi.org/10.1007/s003600050266

Winter, D. A. (2005). *Biomechanics and motor control of human movement*. John Wiley & Sons.

Wu, M., & Gerhart, J. (1991). Raising *Xenopus* in the Laboratory. *Methods in Cell Biology*, *36*, 3–18. https://doi.org/10.1016/s0091-679x(08)60269-1

Wygoda, M. L. (1984). Low cutaneous evaporative water-loss in arboreal frogs. *Physiological Zoology*, *57*(3), 329–337. https://doi.org/10.1086/physzool.57.3.30163722

Young, N., Carter, L., & Evangelista, P. (2011). A MaxEnt model v3. 3.3 e tutorial (ArcGIS v10). Fort Collins, CO.

How to cite this article: Ginal P, Mokhatla M, Kruger N, et al. Ecophysiological models for global invaders: Is Europe a big playground for the African clawed frog? *J Exp Zool*. 2020;1–15. https://doi.org/10.1002/jez.2432